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A MONOGRAPH OF SEPTOBASIDIUM.—PART I. JAMAICAN SPECIES[1]

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Plates 10–25

The material on which the following descriptions of species are based was collected in the Blue Mountain regions of Jamaica, B. W. I., during the summer of 1926. Detailed notes and a good many of the drawings were made in Jamaica while the plants were in the fresh condition. That the writer was able to do this in Jamaica is due to the genius of Dr. Duncan S. Johnson, of Johns Hopkins University, who transformed an old abandoned coffee factory into a well appointed laboratory.

The species have been compared with the collections of *Septobasidium* in the Missouri Botanical Garden Herbarium, in Dr. E. A. Burt's Herbarium, and in the New York Botanical Garden Herbarium. I am particularly indebted to Dr. Burt for identifying the species of *S. jamaicaense* Burt and *S. frustulosum* (B. & C.) Pat. I should also like to acknowledge my gratitude to Dr. W. C. Coker for encouragement and advice.

It is the purpose of the present article to give a summary of the results of my observations on the biology of the genus and to describe the species collected in Jamaica. In a subsequent article other species are to be described and a detailed account of the biology of certain species is to be presented.

Species of *Septobasidium* inhabit the bark and leaves of living trees, shrubs and sometimes herbaceous plants. Von Höhnel (1907) first discovered scale insects beneath the stroma of *Septobasidium* and, finding that the fungus did not penetrate into the tissue of the leaf, concluded that a close biological relationship must exist between the fungus and the scale insects. Regarding the nature of this relationship, he states, "It may be parasitism, or saprophytism, or it may be that a complicated symbiotic relationship exists."

Since his remarkable discovery, the majority of species described

[1] A large part of the work reported in this paper was done while the writer was a National Research Council Fellow in Botany at the Missouri Botanical Garden.

have been found associated with colonies of scale insects, and interest has been directed to the relationship between the fungus and the scale insects. One group of investigators claims that the fungus parasitizes the bodies of the insects, completely overgrowing and finally destroying them (Petch, 1911, 1921, 1927; Burt, 1916; Snell, 1922). Another group claims that the species of *Septobasidium* live saprophytically or epiphytically on the excretions of scale insects (Gäumann, 1926).

As a result of continuous studies for the past two years on several common species around Chapel Hill and studies on the Jamaican material preserved in formol-acetic alcohol, I have found that neither parasitism nor saprophytism adequately describes the relation between *Septobasidium* and the scale insects, but rather that a symbiotic relationship exists. I shall give here merely a summary of the more important results obtained on one species.

In the case of *S. retiforme* (B. & C.) Pat., an exceedingly common species on a great variety of trees and shrubs in the southeastern United States, it has been found that the fungus and scale insects live together in a symbiotic relationship at the expense of the host plant. This fungus-insect relationship is perennial, depending only upon the life of the tree or shrub. The fungus furnishes a home and protection for the insects, so that, shielded from inclement weather and protected from their natural enemies, the insects may suck the juices of the host plant, grow and finally reproduce their young in vast numbers. These young, depending upon the time of year, crawl out toward the margin of the fungus, settle down and some of them repeat the cycle; others are parasitized by the fungus.

The type of parasitism is of a highly specialized nature. The fungus enters the circulatory system of the living insect and there develops numerous exceedingly elaborate coils which absorb food from the "blood" of the insect. A number of insects are finally killed and used up by the fungus, others though infected may survive to reproduce, and some are free from any infection. The fungus also receives some nourishment from the excretions given off by the healthy, uninfected insects; but this amount of food is negligible as compared with that derived from the parasitized insects.

In all other species studied, save the one herein-after reported parasitic on the sporangia of a fern, essentially the same relation exists between the fungus and scale insects as has been found in *S. retiforme*. On plate 24 are shown the several types of haustoria which the various species here described develop in the circulatory systems of the parasitized insects.

In *S. retiforme* the fungus never seems to penetrate into the bark. Evidence for the truth of this statement can be beautifully demonstrated by thoroughly wetting a piece of limb on which the fungus is growing and it is then possible to lift the entire fungus from the bark except where it is indirectly fastened to it through the parasitized scale insects. This is not true for all species of *Septobasidium*. Several species from Jamaica, as described below, do penetrate into the bark, in some species, reaching the living cells. Such species are, however, at the same time symbiotically associated with scale insects. Some species have been reported as destroying the scale insects and then parasitizing the plant (Petch, 1921). "That happens," quoting from Petch, "in the case of an undetermined species on tea in Ceylon, the species which causes the disease known as velvet blight on tea in northern India, and several species on tea and mulberry in Japan."

Owing to the large number and great variety of species which have been described and the fact that in a number of these species the basidia, and in some cases, the probasidia, have not been seen, it is impossible to give a satisfactory comparative discussion of the genus as a whole. It is also quite difficult to satisfactorily separate the genus *Septobasidium* from *Helicobasidium* as indicated by the confusion which has arisen over *Helicobasidium Mompa* Tanaka. It seems best, for the present at least, to follow Patouillard (1900) and have the presence of the probasidial cell in *Septobasidium* and its absence in *Helicobasidium* the chief distinguishing character between the two genera.

A description of the genus follows:

SEPTOBASIDIUM Pat.

Plant body usually resupinate but very variable, dry, crustaceous or spongy. In the commoner species composed of three regions: the subiculum which grows over the bark, the middle region composed of upright slender pillars or thick pillars or mounds or ridges of hyphae which support the top layer in which the hymenium is formed. In some species the context is more or less compact throughout. Threads septate, without clamp connections. Probasidial cell undergoing a long period of rest before germinating, or elongating immediately into the basidium. Basidium usually transversely septate into two or four cells, rarely one-celled, straight or curved. Spores elliptic or bent-elliptic, colorless, becoming divided into two to eight cells soon after formation and budding numerous sporidia if kept moist. Inhabiting the stems, branches or leaves of living woody plants and generally symbiotically associated with scale insects, some of which are parasitized, others of which are left to reproduce; but sometimes directly parasitic on plants.

Widely distributed in the tropics and the warmer regions of the temperate zone.

Patouillard in 1907 described a very peculiar species under the name of *Septobasidium* (*Noackia* nov. subgen.) *scopiforme* nov. spec. This species differed from all others in that instead of having a resupinate structure as a *Corticium* it was composed of a tuft of upright branches in the manner of a *Clavaria* or a *Lachnocladium.* In probasidial and basidial characters the plant resembled *Septobasidium;* and, therefore, in spite of the peculiarity of vegetative structure it was given only subgeneric rank.

Raciborski (1909) studied eight different species of *Septobasidium* and as a result of his studies divided the genus into three genera or subgenera on the ground of the morphological structure of the vegetative body. These groups are: *Ordonia*, in which the vegetative body, as in *Tomentella*, consists of a fine, web-like, undifferentiated layer; *Mohortia*, in which the plant body is composed of two layers, a basal sterile layer over which is formed the hymenial layer; and *Septobasidium* in which, between the basal layer and the top hymenial layer, there is still another region, the middle region, composed of pillars which support the hymenial layer (l. c., p. 360).

It would seem that these three subdivisions, while suggestive, do not help much in arriving at a natural grouping of the various species of *Septobasidium* since they do not take into account the probasidial or basidial characters. In the writer's opinion, they should be recognized as subgenera rather than as genera, as was done by Patouillard with *S. scopiforme.* In attempting to use only the vegetative characters of *Septobasidium* as a basis for generic classification one comes upon an exceedingly peculiar condition. In all the species which the writer has examined, except the species parasitic on fern sporophylls, the fungus is symbiotically associated with scale insects. This association, in some species, is coincident with a high degree of modification in the vegetative structure of the fungus. These sub-hymenial characters are very helpful in separating species, but it would seem hardly logical to split the genus up into several genera on the basis of these vegetative modifications when the probasidia and basidia show such variable peculiarities in development and structure. It would seem much better to follow the line of division established by Patouillard (1892) if the genus must be split.

Patouillard (1892) divided the genus into two groups on the basis of

the development and structure of the probasidium and basidium as follows:

A. Typicae: Entire probasidium elongating to form the basidium. E.g., *S. Michelianum* (Ces.) Pat. and others cited by Patouillard.

B. Gausapia: Probasidium persistent in the form of a globose sac with thickened walls. E.g., *S. pedicellatum* (Schw.) Pat.; *S. Langloisii* Pat.

Patouillard further stated that the basidia might be once to thrice septate.

Key to the Jamaican Species

A. Entire probasidium elongating to form the basidium
  1. Basidium 2-celled
    a. Middle layer composed of abundant, distinct, tall (up to 2 mm.), slender pillars.....*S. jamaicaense* Burt
    b. Middle layer composed of anastomosing ridges of hyphae; context areolate.....*S. areolatum* n. sp.
  2. Basidium 4-celled
    a. Middle layer composed of erect pillars; hymenium thin, papery *S. papyraceum* n. sp.
    b. Middle layer composed of exceedingly broad anastomosing ridges of hyphae; hymenium with dichotomously branched and coiled hyphae.....*S. frustulosum* (Berk. & Curtis) Pat.

B. Probasidium persisting in the form of a globose or subglobose sac
  1. Basidium 4-celled
    a. Middle layer composed of pillars which are very short; hymenial layer with numerous small black dots.....*S. atropunctum* n. sp.
    b. Middle layer irregularly honey-comb like, alveolate *S. alveolatum* n. sp.
    c. Middle layer compact; on fern sori.....*S. Polypodii* n. sp.
  2. Basidium one-celled, bearing one spore *Septobasidium* (*Unisporum* n. subgen.) *purpureum* n. sp.

Septobasidium jamaicaense Burt

Plates 11, 15, 16, 23, 24

Plant body resupinate, often stratose, often covering an area of several square decimeters on the bark of living trees; up to 1 cm. thick in large fresh specimens, drying down to 2–4 mm. thick. Plants usually consist of two distinct regions: the very thin, byssoid, marginal, vegetative region and the thick, fruiting region. Marginal region up to 3 cm. wide, composed of numerous blackish brown rhizomorphs with a purplish tint, from which branch out a delicate sheen of mycelial threads; rhizomorphs and threads closely adherent to the bark, but separable from it when wet. Fruiting region smoke gray or pale neutral gray over a

bister or bone brown context. In section composed of three layers: (1) the subiculum, which runs horizontally over the bark, and is composed of numerous very conspicuous rhizomorphs and mycelial threads, 100–300μ thick and from which the pillars arise in vast numbers; (2) pillars nearly straight and perpendicular in the growing region of young plants but becoming considerably entangled, passing obliquely from the subiculum to the hymenium, sometimes branched, very variable in diameter, sometimes composed of as few as three threads and then about 6.2μ thick, often up to 60μ thick, rarely up to as much as 180μ, most 20–30μ thick; single pillars very long, often 2 cm.; threads of pillars about 3.7μ thick, rarely branched, septate without clamp connections; pillars branching and then the branches breaking up into single hyphae as the pillars approach the hymenium; (3) hymenium compact in certain areas, hypochnoid in others, showing clusters of the spore-bearing organs, 70–100μ thick, composed of probasidia borne laterally in various stages of development; subglobose, varying in size from the youngest initial bud up to the fully mature basidium, 8–14 $\times$ 40–62μ, straight, once septate, a transverse partition thus giving the "basidium" the appearance of a teleutospore of *Gymnosporangium macropus*, each cell sprouting a long sterigma on the end of which is borne a long spore which is more or less pointed at both ends and distinctly recurved at the distal end; spores white, 6.8–11 $\times$ 23–39μ, including the bent end, most about 8 $\times$ 27μ; usually becoming thrice septate and not rarely seven times septate; often forming, after the septation process is complete, numerous little spores by a budding process.

Associated with colonies of scale insects, some of which are parasitized by much gnarled, irregular coils of hyphae, others of which are not parasitized (plate 24, fig. 6). Scale insects very abundant and evidently the primary direct source of injury to the trees. On *Solanum punctulatum*, Jamaica, B.W.I.

This species has apparently been collected only once before and was then found in Jamaica in the Blue Mountain region, "John Crow Peak," at an altitude of 5500 feet, in April by Dr. L. M. Underwood. It was first described by Dr. E. A. Burt ('16) from Underwood's material and was very appropriately named *S. jamaicaense* since I have later found this species to be by far the commonest in Jamaica. My material has been seen by Dr. Burt and has been compared with his type material and agrees. Dr. Burt gives the spore size as 13 $\times$ 5$\frac{1}{2}\mu$, which is much too small. The shape of the spore in his figure is also incorrect since the bent end of the spore should be opposite the mucro end.

Out of eighteen collections from various localities seventeen are on the bark of *Solanum punctulatum*, the eighteenth is on the bark of a species of *Psychotria*. My collections were taken from Portland Gap,

on various locations around Blue Mountain Peak, ravines on the sides of Mossman's Peak, Cinchona, the Mabess Valley and Hardware Gap. *Solanum punctulatum* also occurs at Mandaville, which is in the lowlands; it would be of interest to know if the fungus also occurs there.

This species can be distinguished by its very thick and extensive growth, by its habitat on *Solanum punctulatum*, by the dark brown mycelium with a faint purplish tint when fresh (when dry the purplish tint almost or entirely disappears), and the grayish slate colored hymenial surface in which the probasidia are so often borne in minute clusters. In actively growing specimens the marginal region with its extensive rhizomorphs is very distinctive.

Field observations on this species showed that the fungus-scale insect combination did considerable damage to the host, *Solanum punctulatum*. The fungus often covers the bark on the leeward side of trees for areas of several square decimeters and in a few specimens was seen to extend from near the base of trees as much as thirty feet high almost to the top. Rarely in deeply shaded gaps or ravines small trees were seen girdled by the fungus. Such heavily infected trees were usually quite unhealthy, showing a large number of dead limbs. When the fungus was found on dead limbs or dead trees, it also was dead. The following illustration of this was brought to my attention. On the north side of Portland Gap in the Blue Mountains of Jamaica there occurred a large land slide several years ago. Many trees of *Solanum punctulatum* were uprooted by the slide, and most of them are now dead. The fungus was abundant on many of the dead trees and was invariably dead itself. Another striking illustration is afforded when the main trunk and a small branch are infected at the junction of the two. If, as is often the case, the small branch is girdled by the fungus and dead, then the part of the fungus on the small branch is also dead while the part of the fungus on the main trunk which is still living, is alive.

Septobasidium areolatum n. sp.

Plates 11, 14, 15, 16, 23

Plant body resupinate, growing extensively over the bark of living trees and often forming an area of as much as 60 sq. cm. Deep rich brown over the vegetative portion, the hymenium grayish. Entire surface marked with numerous holes which are 0.2–0.6 mm. in diameter and 1 to 3 mm. apart. Margin indistinct, except with a lens, often indeterminate, irregular, thin and byssoid. In section up to 2 mm. thick when fresh, about 1 mm. thick when dry, often stratified by

the formation of several hymenia over the same area. Composed of three regions: (1) subiculum, about 20–45μ thick, which grows over the surface of the bark and very noticeably penetrates into the phellogen cells destroying their contents and walls; (2) the middle region, 0.8–1.5 mm. thick, composed of brown, loosely packed, branched threads which extend in all directions, threads 3.5–5μ thick, septate, without clamp-connections; (3) the hymenial region, which is about 40μ thick, and composed of probasidia and basidia in various stages of development and of delicate branched hyaline threads, the extensions of the coarser brown threads; probasidia spherical or subspherical, with a slightly thickened wall, 10–12.6μ thick, elongating into an irregularly cylindrical, once septate basidium, each cell of which sprouts a long sterigma and bears on its end a spore. Basidium 8–10 $\times$ 24–33μ, sterigmata 12–25μ long or sometimes longer; basidium as in *S. jamaicaense* except smaller. Spores bent-elliptic, bent like a fish hook, the bend being opposite the mucro, 5.5–6.8 $\times$ 25–30μ, usually becoming thrice septate.

Collected twice on bark of a living deciduous tree, symbiotically associated with scale insects. Many insects were dissected out from beneath the stoma of the fungus which were not parasitized; others, however, were parasitized by very irregular coils of hyphae. No fine threads were present. Mossman's Peak, Blue Mountains, Jamaica, B.W.I., July, 1926.

The basidia of this species closely resemble those of *S. jamaicaense* but the two plants can readily be separated on vegetative characters.

The small and numerous areolations, the rich brown color contrasting with grayish hymenium when present, and the absence of pillars characterize the plant. The areolations are formed in an interesting way. In the absence of upright pillars the middle layer is formed by the development of ridges of hyphae which arise from the subiculum. These ridges branch and anastomose with each other thus forming a network of ridges. The hyphae at the top of the ridges grow out horizontally parallel with the subiculum. This growth always ceases before the space between the ridges is completely bridged and thus the little holes (areolations) in the upper layer are formed.

The hyphae of this species penetrate deeply into the periderm of the bark and develop extensively there. Penetration is most extensive underneath the old, dead remains of scale insects.

Septobasidium papyraceum n. sp.

Plates 10, 15, 17, 23, 24

Plant body resupinate, usually forming very large irregular patches on the bark of living trees, often girdling the limbs and extending for

several decimeters, the hymenial surface resembling a *Corticium*. Surface of fruiting areas smooth in the fresh condition, becoming somewhat wrinkled upon drying, margin of hymenium often incurved, thus forming cup or saucer-shaped fructifications of the small hymenial patches. Entire thallus composed of three distinct areas: (1) the very thin lower layer or subiculum, which extends over the bark and is nearly inseparable from it, subiculum purplish or purplish brown with a narrow whitish margin when fresh; (2) the middle region of upright brownish pillars which arise in irregularly scattered clusters, each cluster of pillars arising from a basal, brownish pad, pillars composed of a few to many parallel threads 8–45μ thick, threads of pillars 3–3.8μ thick, septate without clamp connections, pillars giving rise above to the upper byssoid layer on which the hymenium develops. Hymenium silvery drab to pinkish drab, thin, papery, with an exceedingly compact texture, easily separable from the pillars, 40–50μ thick, composed of probasidia and basidia in various stages of development and slightly coiled threads; threads 3–3.8μ thick, probasidia spherical to oval, 7.4–11.2μ thick, wall not perceptibly thickened, elongating and growing to form the basidia which are 50–60μ long, irregular in thickness and considerably twisted, becoming divided into four cells from each of which a long sterigma grows. Spores 6.6–8.5 $\times$ 18–22.5μ, distinctly recurved and papillate at the distal end, becoming usually two-celled but also not rarely four- or eight-celled.

This species was found three times in the Blue Mountains on the bark of living *Psychotria* trees. Associated with scale insects, many of which are parasitized by irregular coils of hyphae, and others of which are not parasitized (plate 24, fig. 5).

This fungus is easily recognized by the thin, paper-like hymenium with its pinkish drab or silvery drab color which shows a striking contrast to the much darker, brown pillars and subiculum.

Septobasidium frustulosum (Berk. and Curtis) Pat.

Plates 12, 15, 17, 24

Plant body resupinate, growing in medium sized, effused patches, olive-ochre to old gold, with numerous narrow (about 0.1–0.3 mm. wide) sinuous, anastomosing cracks, and sometimes in young specimens with numerous pinholes; margin indistinct, byssoid, concolorous with the context or slightly lighter. In section 0.6–1 mm. thick, composed of three layers: (1) a lower, compact, thin layer of entangled, matted threads which run more or less parallel to the substratum (this layer as a layer is often rather indistinct or entirely absent) about 35–50μ thick; (2) the middle layer of loosely packed, much entangled and branched threads about 2μ thick, arising from the lower layer and passing upward, without the formation of pedicels, to form the hyme-

nium, middle layer 300–550μ thick, broken by numerous connecting channels; and (3) the hymenial region which varies from a few microns thick in the young regions of growth up to 300–370μ thick in the older regions; hymenium stratose by the formation of densely packed layers of basidia; basidia also formed in between the strata, i.e., scattered throughout the hymenial region; hymenial region composed of very densely packed hyphae which are many times dichotomously branched, threads 0.8–1μ thick, the ends of the branches curved backward and often spirally coiled; pyriform probasidia, about 6 $\times$ 15μ, borne laterally on the hyphae, developing into a much twisted, usually four-celled basidium; sterigmata formed from each cell and bearing a single elongated spore. There are also found in the hymenial region numerous, two or three times septate, sausage-shaped bodies, which are either terminal or intercalary. Spores elliptic (only a few immature ones seen).

Collected twice on the bark of living deciduous trees near Cinchona, Jamaica, B.W.I., July, 1926. Associated with scale insects, many of which are parasitized by peculiar hyphae (plate 24, fig. 3). These latter are composed of clavate segments, which are about four to five microns thick at one end and taper down to a fine thread at the other, the fine thread almost always connecting with the larger end but at times the fine thread may arise from the smaller end. The smaller end of the segments are always septate. Such hyphae branch considerably. Other insects, however, are not parasitized. This species is easily distinguished by the olive-ochre to old gold color, by the absence of supporting pillars, by the anastomosing cracks in the fruit bodies, by the dichotomously branched and coiled threads in the hymenium, by the coiled basidia, and by the peculiar, elliptic, septate bodies in the hymenial region.

Septobasidium atropunctum n. sp.

Plates 13, 15, 18, 23

Plant body resupinate, forming a thin, closely adherent crust over the bark, usually girdling the limb and extending for a decimeter or more along its length. Surface rather smooth in the younger areas, becoming cracked in older regions; cinnamon brown with numerous black dots (the coverings for the scale insects) which are 0.3–1 mm. wide. Margin 2–3 mm. wide, byssoid, whitish. In section, 175–265μ thick, composed of three layers: (1) subiculum 50–65μ thick, composed of a dense layer of hyphae which lie next to the bark; (2) the middle region 150–200μ thick, composed of upright hyphae which are grouped in large loose clusters forming thick pillars and leaving small spaces in

between the pillars; (3) hymenial region 30–60μ thick, composed of branched sterile hyphae and probasidial cells, probasidial cells 11.8–14μ thick, wall considerably thickened, spherical or slightly subspherical, sprouting under favorable conditions to form the basidia, the former emptying its entire contents into the latter during the process. Basidia 4.6–5.4 $\times$ 58–70μ, long, narrow, cylindrical, becoming thrice septate, each of the four cells thus formed giving rise to a sterigma which bears a spore. Spores 3–4.2 $\times$ 16–22.5μ, bent-elliptic, usually becoming once or thrice septate, though if kept moist often becoming divided into eight cells.

This species was collected from two localities near Cinchona, Jamaica, B.W.I., on the bark of living trees. Associated with scale insects, some of which are parasitized by irregular coils of hyphae while others are not parasitized.

This is an exceedingly interesting form since it shows an obvious and rather high degree of specialization on the part of the fungus in adapting itself to the needs of the scale insects. The fungus forms a little, flattened, oval-shaped house for the scale insects. The floor is considerably depressed so that the roof is even with the surface of the fungus. The roof is made of an exceedingly compact layer of hyphae and is nearly black in color. One end of the roof is free, thus leaving an entrance. This free margin is fringed with whitish hyphae so that the opening is quite conspicuous under a binocular microscope. If the roof is lifted, nearly every house is found to contain a scale insect. It is only in the marginal regions where the fungus is developing that the houses with "open doors" are found. In the older regions the growth of the fungus has pushed up around the roof and thus more or less closed the entrance. The majority of these older houses are empty, containing nothing but the large, old insects' shell. In a few of these old empty shells, the dried bodies of young were found which were absolutely untouched by the fungus. The new houses contain only small, young scale insects.

It is obvious, although these observations were made on material which I had collected two years previously and on which I was therefore unable to follow the behavior of the living insects, that the young hatch out in the older houses and crawl out of the ones that are not completely closed, migrate out to the marginal region, enter the little houses, and there develop their sucking organs which penetrate the tree for food. In return for this protection the fungus parasitizes many of the insects.

Septobasidium alveolatum n. sp.

Plates 14, 15, 19, 23, 24

Plant body resupinate, forming irregular patches on the bark of living trees, 1 to 3 or more centimeters wide by a few to 10 or 15 cm. long, blackish with a little brown over the vegetative portion, the hymenium grayish. Surface of vegetative part areolate, spiny, presenting as a rule an irregular, finely honey-comb appearance. Hymenium forming over the areolated areas, at first in very small patches, which sometimes anastomose to form a continuous hymenial surface for several square centimeters; hypochnoid at first, becoming compact and smoother with age. Margin very indistinct and irregular, apparent only with a hand lens. In section up to 3 mm. thick when fresh, usually 1–2 mm. thick. Composed of three regions: (1) a very thin inconspicuous subiculum, which creeps over the surface of the bark following especially the cracks and penetrating by means of the cracks as far as the cork cambium; (2) the middle region composed of very loosely packed, slightly wavy hyphae, which are not arranged in pillars or pedicels but in enormous columns; threads dark brown under microscope, septate without clamp-connections, 4–5.4μ thick; (3) the hymenial region which is exceedingly variable in thickness, when well formed from 60–120μ thick, but in old specimens up to 250-350μ thick; composed of probasidia and basidia in various stages of development and numerous hyaline, branched, wavy threads (3.5–4.3μ thick) from the sides of which the former arise. Probasidia spherical or subspherical, 14–17μ thick with a slightly thickened wall, which is as a rule thicker on one side than the other, developing into the basidia by sprouting and emptying its entire contents into the latter; basidia long-cylindrical, usually slightly curved or twisted, rarely straight, becoming divided by transverse walls into four cells, each cell sprouting a sterigma which bears on its end a large spore. Spores white in print, elliptic to bent elliptic, 7.4–11.7 $\times$ 18–29μ, becoming once septate a few hours after formation.

Quite common, collected eight times on the bark of living *Psychotria* sp. and other deciduous trees and often overgrowing epiphytic, mosses and liverworts. Portland Gap, Blue Mountain Peak, Mossman's Peak, and Cinchona, Jamaica. June, July 1926. Associated with scale insects, some of which are parasitized by very irregular coils of hyphae, and segmented hyphae, the segments being connected by fine hyphal threads like strings of sausages (plate 24, fig. 2.) Many insects, however, are not parasitized.

This species in appearance to the unaided eye is nearest *S. cirratum* Burt. The color in some specimens of the two plants is practically identical. A careful examination serves, however, to show unmistakable differences in the two plants: *Septobasidium cirratum* in most

specimens shows a much more effused, continuous and compact growth; young specimens, but old enough to be fruiting, strikingly resemble a small foliose lichen with lighter colored and upturned margins; young areas spreading vegetatively over the bark do not show the honeycomb appearance so characteristic of this present form. A comparison of sections under the microscope shows even more distinct differences. The context of *S. cirratum* is very compact, that of *S. alveolatum* very loose. In the surface of *S. cirratum* are numerous coiled threads; these are absent in *S. alveolatum*. The basidium in *S. cirratum* is formed by an elongation of the probasidium forming part of it and is 2-celled, while in *S. alveolatum* the basidium is 4-celled and sprouts from the probasidium which becomes empty and does not form part of the spore-bearing body.

From *S. Langloisii* it can easily be distinguished by the much lighter color of that species, and by surface and basidial characters.

The shape and structure of the probasidia and basidia of the present species suggests a likeness to Patouillard's figures of *S. pedicellatum* (Journ. de Bot. **40**:61. 1892). Patouillard's figures show oval probasidia, while the probasidia of the present species are usually spherical or slightly subspherical. The present species often overgrows mosses and lichens as Burt describes for *S. pedicellatum* (Ann. Mo. Bot. Gar. **13**: 330. 1926), but this is of no specific value in the present case, since so many specimens are free from mosses and lichens. The type material for *S. pedicellatum* is in the Museum of Paris and is therefore unavailable to me for comparison. However, Dr. Burt very kindly loaned a slide showing sections of authentic *S. pedicellatum*, and in these sections the pillars supporting the hymenial layer were very distinct, while in the present species the subhymenial layer has a honeycomb-like structure. Furthermore, in the hymenium of *S. pedicellatum* there were numerous very delicate threads about 1–1.2μ in diameter, whereas the threads in the hymenium of the present species are 3.5–4.3μ thick. The color of the two plants, moreover, is different: in *S. pedicellatum* the color is avellaneous; in the present species the fertile areas are cinereous, the unfertile areas black. I have also examined a collection of *S. pedicellatum* (Schw.) Pat. collected by Earle in Porto Rico on living orange bark (No. 67, N. Y. Bot. Gard. Herbarium). This material agrees well in most respects with Patouillard's and Burt's descriptions. It is avellaneous in color over the hymenial region, and has distinct pillars. In the hymenium are the small threads mentioned by Burt. The probasidia are abundant and agree in shape with Patouillard's drawings but his measurements are considerably larger than are the probasidia in Earle's

collection. *Septobasidium pedicellatum* as represented in Earle's collection differs distinctly from the present species.

Septobasidium Polypodii n. sp.

Plate 20

Plant body resupinate, overgrowing and completely covering the undersurface of fertile fronds of *Polypodium* sp. and parasitizing the sori. Nearly white when fresh, becoming cream-colored upon drying. In section, 250–700μ thick, usually about 500μ thick at the thickest part, whitish throughout, composed of (1) a very thin, lower layer of hyphae which extend over the lower surface of the fern leaf but do not penetrate into the epidermal tissue; and (2) a layer of compact, much branched, coiled and entangled hyphae arising from this lower layer, often stratose by the successive formation of two or three fruiting regions. No pillars present. Probasidial cells formed in the outer surface of the compact layer, oval, 12.5–14.8 $\times$ 16–23μ, wall slightly thickened, germinating into a four-celled, coiled (about in the form of a semicircle) basidium, 8.2–12.6 $\times$ 50–70μ, which in turn bears four spores. Spores elliptic, 6.5–8.5 $\times$ 19–25μ, becoming once septate.

Collected once on *Polypodium* sp. in the Blue Mountains of Jamaica, B.W.I., June, 1926.

This species is distinguished from others by its growth on fern sporophylls, and the absence of scale insects beneath the stroma. It is also conspicuous by the absence of pillars.

When the material was collected it was passed over at the time without much study and was not recognized as a *Septobasidium* until nearly two years later. I am therefore unable to make a full and certain report as to the fungus host relationship. A study of sections made of several infected sporophylls has shown no scale insects underneath the fungus. The fungus starts its development on the naked sori, covering the developing sporangia and their stalks with a mat of hyphae. In several instances cases of penetration by the fungus into the pro-sporangial cells could be made out. The fungus does not penetrate at all into the vegetative parts of the fern sporophyll. In spite of the obvious parasitism a good many of the sporangia mature, forming apparently good spores.

Septobasidium (Unisporum n. subgen.) **purpureum** n. sp.

Plates 12, 15, 21, 24, 25

Plant body resupinate, often covering an area of one to several square decimeters on the bark of living trees; brownish with a purplish tint

except where the hymenium is developed and then dull, neutral gray. Surface in older regions cracked by irregular fissures. Margin indeterminate. In section 300–700μ thick, not distinctly differentiated into layers, pillars absent. Threads of context much branched and entangled, septate without clamp connections, about 3.8μ thick, deep brown under microscope. Hymenium indeterminate, the basidia apparently being formed perennially, the old, empty, probasidial cells scattered throughout the context, the younger probasidial cells and basidia near the surface. Probasidial cells spherical, 8.5–13.8μ thick, usually about 10μ thick, remarkable in having a wall which is much thickened in one-half and very thin in the other; sprouting into a cylindrical basidium which immediately gives rise to a long sterigma on the end of which is borne a single spore. Basidium 6.6–8.4 $\times$ 14.7–25μ, usually thickest in the middle or at the distal end; without septa, but separated from the empty probasidial cell by a wall, sterigma usually apical, rarely lateral, about half as long as the basidium. Spores 7.4–10.4 $\times$ 15.5–19.6μ, elliptic, slightly flattened on one side, pointed or rounded at the distal end, usually becoming divided into eight cells by transverse and longitudinal septa.

Collected twice (Nos. 143 and 146) near Cinchona, Jamaica, B.W.I., July, 1926. On the bark of living deciduous trees; symbiotically associated with scale insects, many of which are parasitized by peculiar, spindle-shaped segments of hyphae, the segments being connected end to end by fine threads, thus resembling strings of sausages (plate 24, fig. 1; and plate 25). Other insects, however, are not parasitized. This species may be recognized in the field by the striking color, thin context, and absence of pillars. In section the non-septate basidium which bears a single spore characterizes the species.

This peculiar species because of the non-septate basidium which bears a single spore, obviously does not belong in the section of the genus *Septobasidium* with *S. pedicellatum* and the other species with septate basidia. Its symbiotic association with scale insects, habit of growth and the structure and development of the probasidia, basidia, and spores, excepting alone the non-septate basidia, show a very close relationship to *Septobasidium*. I am, therefore, establishing a new subgenus to include this species.

A very striking observation, in the species of *Septobasidium* studied by the writer, is that in the species in which the basidium is divided into four cells, as in *S. alveolatum*, the spores are normally only once septate and thus two-celled; and in the species in which the basidium is two-celled, as in *S. jamaicaense* Burt, the spores are normally four-celled; while in the present species, the basidium is one-celled and the spore is

eight-celled. The regular septation in the spores occurs shortly after they are discharged if kept in a moist chamber; if, however, the spores are kept in water the septations are quite irregular and if kept in a nutrient solution or on agar they form many sporidia by budding.

Helicobasidium arboreum n. sp.

Plates 14, 15, 22, 23, 24

Plant body resupinate, forming rather thin, cracked areas on the bark of living trees; largest areas up to about 6–8 sq. cm. in extent. Unfertile areas blackish brown, myceloid. Hymenial surface light gray, forming a more or less cracked and granulated surface over the much darker colored, subhymenial hyphae. In section composed of (1) the vegetative hyphae which penetrate throughout the cortex region developing particularly in the cells of the cork cambium and phloem, intracellular hyphae colorless; (2) the superficial vegetative hyphae, which are very dark colored, septate without clamp connections, very loosely packed, 4–8.4μ thick close to the base, not arranged in pillars but arising individually and branching many times to form a dense cluster of hyaline, delicate, coiled and twisted hyphae. Hymenium composed of these clusters of hyphae among which are borne the spore-bearing bodies or basidia. Basidia not arising from an obviously pre-formed resting cell. Mature basidium one to one and one-half times coiled, and thrice septate, 4.8–7.4μ thick by 33–40μ long. From each of the four cells of the basidium a long sterigma grows to the hymenial surface and bears a long, narrow, elliptic spore, distinctly bent at the distal end and usually once septate but not rarely three times septate; spores 5–5.9 $\times$ 21–30μ, white in a spore print.

Collected only once and then on the bark of a living deciduous tree on the Blue Mountain Trail, Jamaica, June 1926. Associated with scale insects, many of which are parasitized by irregular, bent spindle-shaped segments of hyphae which are connected by fine threads (plate 24, fig. 4). Many insects, however, are not parasitized.

This species can be recognized with the unaided eye by the gray color and peculiar granulated surface of the hymenium. In microscopic section the thick dark colored hyphae arising individually and branching to form a dense cluster of hyaline, delicate, twisted hyphae and the coiled basidia are distinctive. I am calling this species *H. arboreum* because of the rather striking similarity of the thick, single, upright hypha with its apical branches to the shape of the stem and branches of a tree.

EXPLANATION OF PLATES

PLATE 15

All figures on this plate are semi-diagrammatic. All figures ×33, except Fig. 1.

Fig. 1. Section through very thick region of *S. jamaicaense* Burt, where four hymenial regions had been formed. ×6.

Fig. 2. *H. arboreum*, showing the tree-like clusters of hyphae.

Fig. 3. *S. atropunctum*, showing the thin hymenium and the short pillars and threads penetrating into the crevices of the bark.

Fig. 4. *S. areolatum*, showing holes (areolations) in context covered here by the hymenium. Note the scale insect with its sucking apparatus penetrating the wood.

Fig. 5. *S. papyraceum*, showing thin erect pillars and part of a scale insect to right.

Fig. 6. *S. frustulosum*, showing exceedingly thick columns of hyphae, and hymenium with dichotomously branched, coiled hyphae.

Fig. 7. *S. purpureum*, showing context without pillars, etc. Note scale insect to right with sucking apparatus extending down into the wood.

Fig. 8. *S. alveolatum*, showing an alveolus covered by the hymenium. Note empty scale at bottom of fungus.

PLATE 16

S. jamaicaense. Figs. 1–5.

Figs. 1–4. ×873. Probasidium, the small body on left, and basidia in various stages of development. Fig. 4 shows an empty basidium with two long sterigmata. Fig. 5. Spores with sterigmata and one sporidium, abnormal. ×720.

S. areolatum. Figs. 6–15. All ×873.

Figs. 6–13. Development of basidium from the stage when it becomes septate to the empty basidium.

Figs. 14, 15. Spores, fig. 14 an abnormal one.

PLATE 17

S. papyraceum. Figs. 1–14. All ×847.

Figs. 1–14. Development of basidium from the probasidium up to the formation of sterigmata. Fig. 14. A basidium which has fallen from the parent hypha.

S. frustulosum. Figs. 15 and 16. ×847.

Fig. 15. Basidium with four sterigmata.

Fig. 16. Part of the hymenium showing dichotomously branched hyphae, probasidia, and coiled basidia, one with a spore. Note also the septate bodies, perhaps gemmae.

PLATE 18

S. atropunctum. Probasidia and basidia in all stages of development; pillars and subiculum. ×558.

PLATE 19

S. alveolatum. All ×873. Development of probasidium into the basidium and the formation of spores.

PLATE 20

S. Polypodii. Section of infected sporophyll, below, showing how the fungus grows in and around sporangia. ×37. Above, section of hymenium showing probasidia and basidia. ×1012.

PLATE 21

S. purpureum.

Figs. 1–11. Development of probasidium into basidium which bears a single spore. ×1016.

Figs. 12–14. Showing how spores if kept moist may divide into eight cells. ×1280.

PLATE 22

Helicobasidium arboreum. All ×1310.

Fig. 1. Basidium and coiled threads borne on very thick hypha.

Figs. 2–6. Basidia, figs. 4 and 5 showing sterigmata.

Fig. 7. Spore sprouting two sterigmata, which is unusual.

PLATE 23

Spores.

Fig. 1. *S. atropunctum* ×578; Fig. 2. *Helicobasidium arboreum;* Fig. 3. *S. alveolatum;* Fig. 4. *S. jamaicaense;* Fig. 5. *S. papyraceum;* Fig. 6. *S. areolatum.* Figs. 2–6 × 982.

PLATE 24

Fig. 1. Haustoria from within body of a parasitized scale insect beneath *S. purpureum.* Haustoria consisting of spindle-shaped segments of hyphae connected by fine threads, like strings of sausages.

Fig. 2. Haustoria from within body of a parasitized scale insect beneath *S. alveolatum,* consisting of sausage-shaped hyphae and irregular coils of hyphae.

Fig. 3. Haustoria from within body of a parasitized scale insect beneath *S. frustulosum.* Note cross wall at the smaller end of the segments.

Fig. 4. Haustoria from within body of a parasitized scale insect from beneath *Helicobasidium arboreum.* Note how the segments are entangled and how almost every segment is bent.

Fig. 5. Haustoria from within body of a parasitized scale insect from beneath *S. papyraceum.* Haustoria consist of more or less regularly coiled hyphae.

Fig. 6. Haustoria from within body of a parasitized scale insect from beneath *S. jamaicaense.* Haustoria consist of irregular coils of hyphae. All figures ×952.

PLATE 25

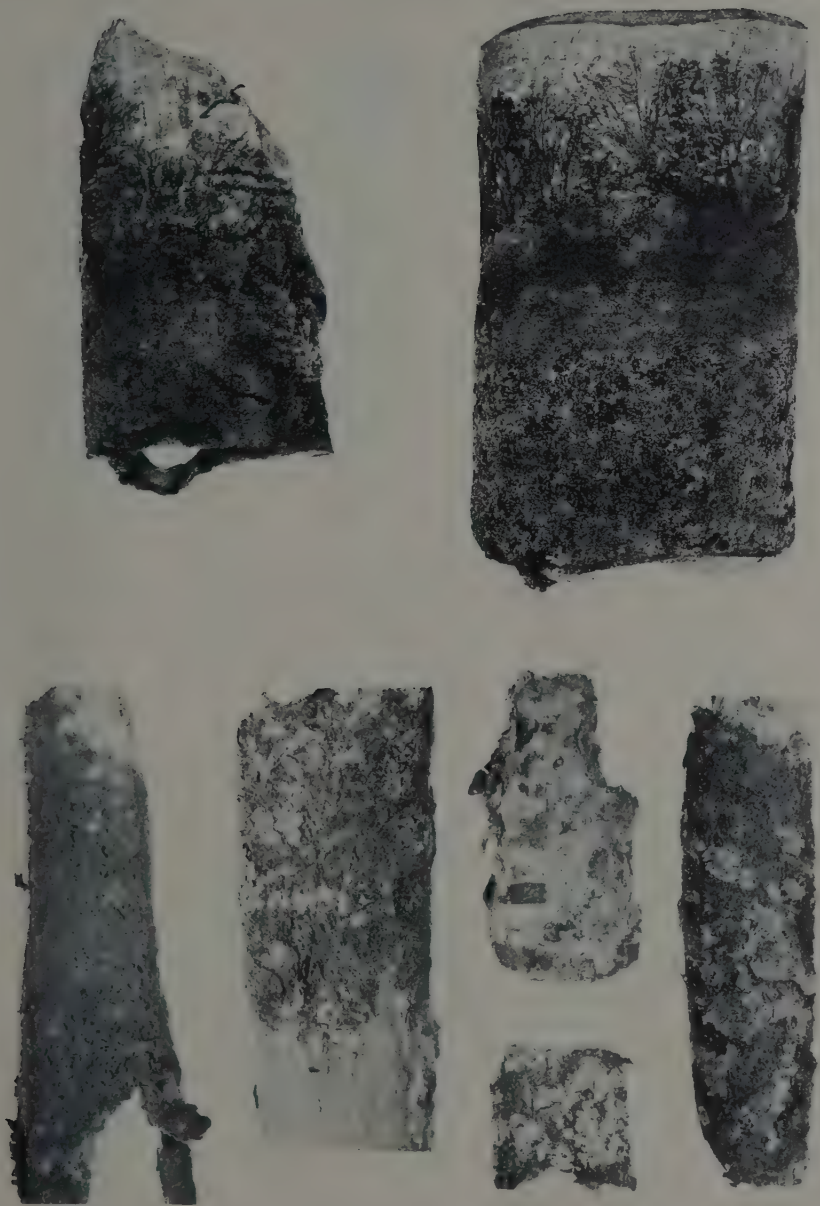
Semi-diagrammatic view of section of *S. purpureum* showing a parasitized scale insect over which the fungus has developed a dense pad of hyphae and the host plant into which the insect's suctorial apparatus penetrates. *P.B.*, probasidia; *B*, basidia; *B.S.*, basidiospores; *O.B.*, old collapsed basidia; *H.P.*, hyphal pad; *D.S.*, insect's dorsal scale; *.VS.*, ventral scale; *I.*, insect; *P.A.*, insect's pumping organ; *S.A.*, insects suctorial "tube" represented by the two middle solid lines; *H.S.*, sheath of cellulose material secreted around the suctorial apparatus; *M.R.*, medullary ray cells; *N.*, nuclei of host plant; *H.*, haustoria of the fungus inside the body of living insect. ×135.

PLATE 10

SEPTOBASIDIUM PAPYRACEUM

Note the small circular patches of pillars on the piece to the left and second from the right. Under each is a scale insect. The hymenium is whitish. Photograph by Paul F. Shope.

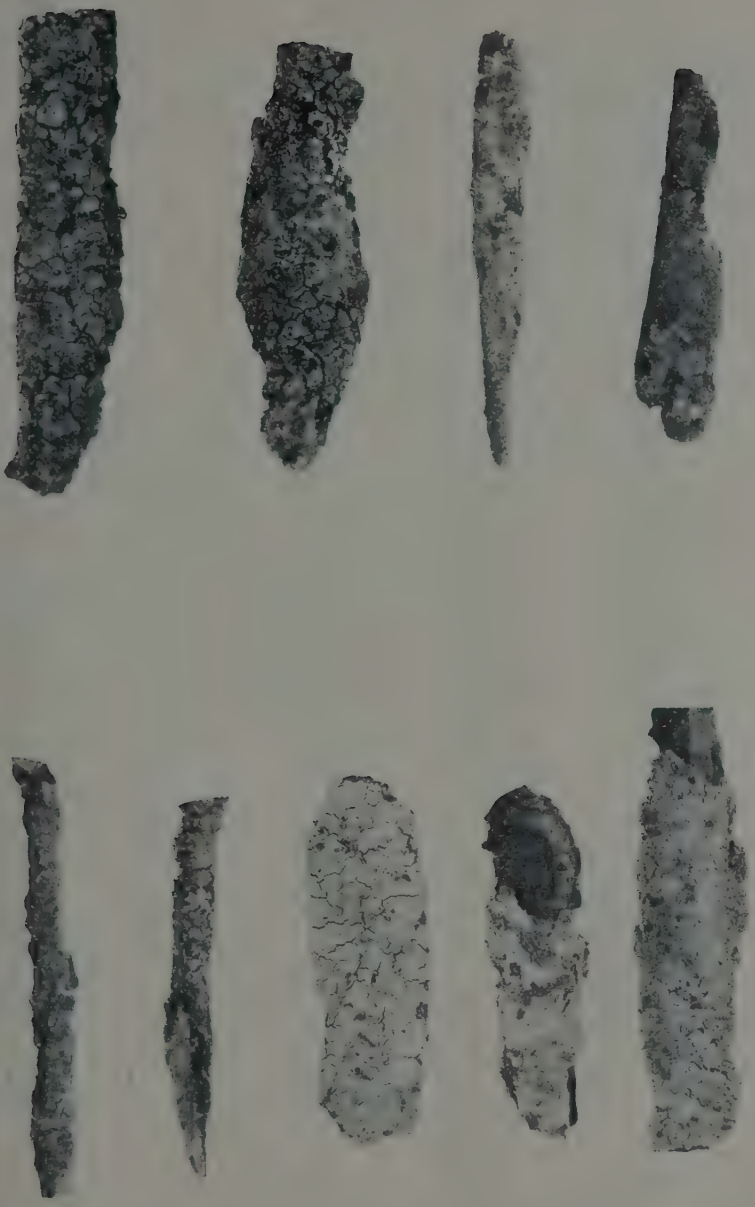
PLATE 11



SEPTOBASIDIUM JAMAICAENSE [above]
Note the distinct rhizomorphs

SEPTOBASIDIUM AREOLATUM [below]
Note areolations. The grayish areas are hymenium. Photograph by Paul F. Shope.

PLATE 12

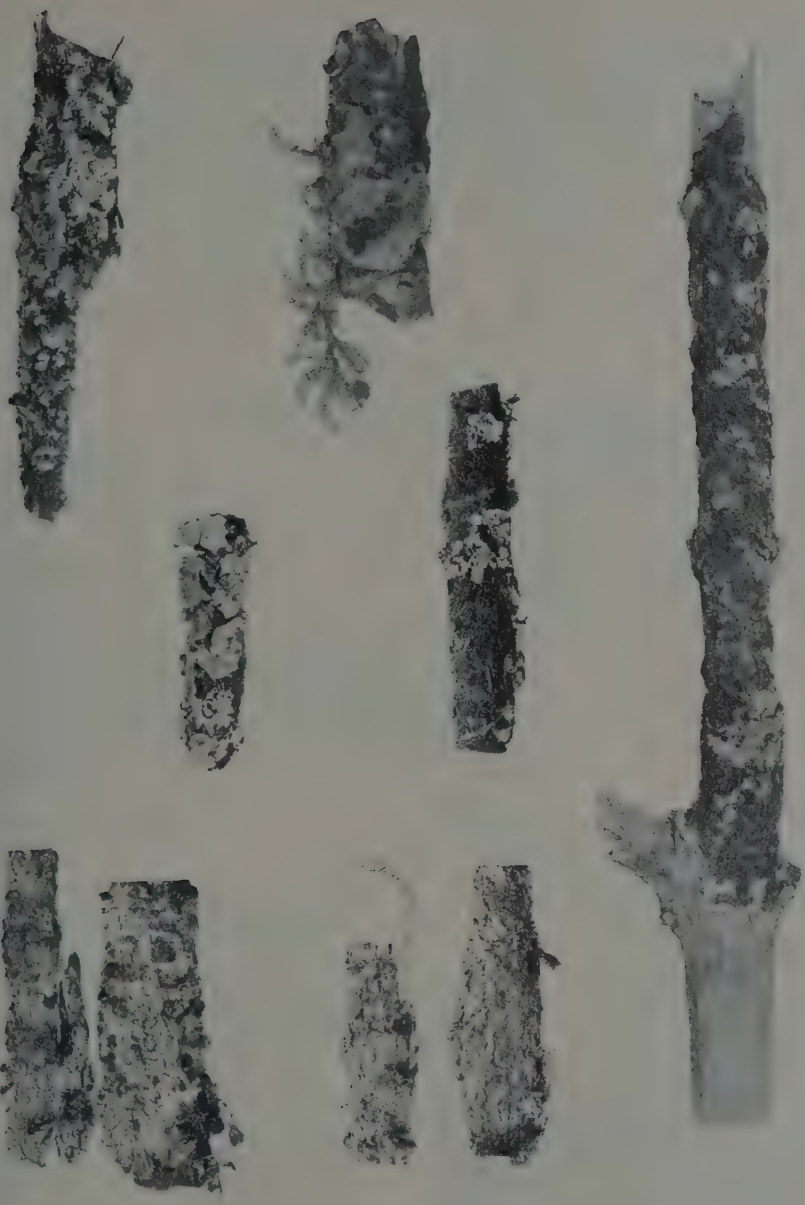


SEPTOBASIDIUM PURPUREUM [above and two pieces on left below]
SEPTOBASIDIUM FRUSTULOSUM [three pieces on right below]
Photograph by Paul F. Shope

PLATE 13

SEPTOBASIDIUM ATROPUNCTUM

Note the minute dark dots on the piece to right near bottom and next piece near top. Photograph by Paul F. Shope.



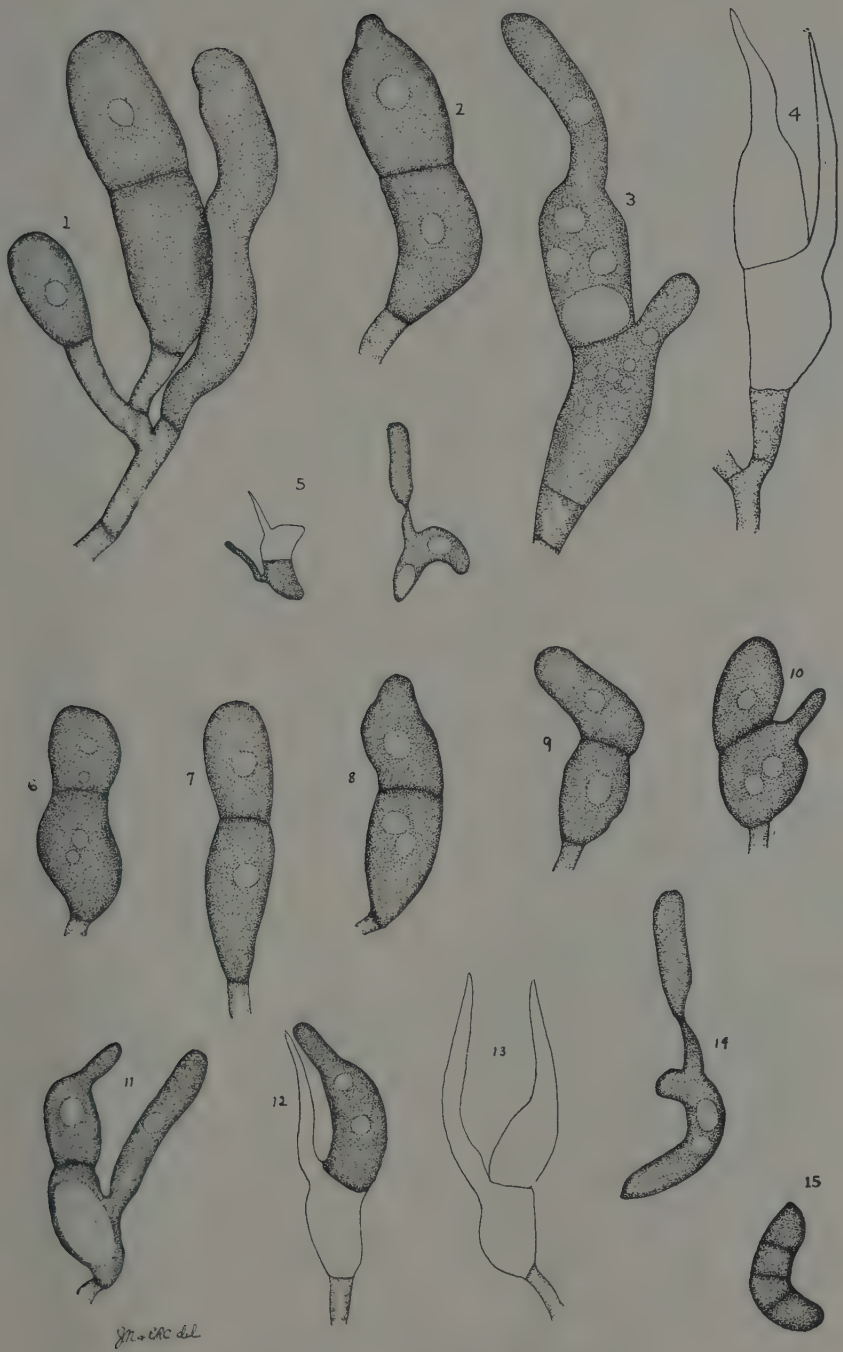
SEPTOBASIDIUM ALVEOLATUM [top, middle and right]

Note the irregularly honey-comb appearance of the piece to the right. The grayish areas are hymenium.

HELICOBASIDIUM ARBOREUM [four pieces on left below]

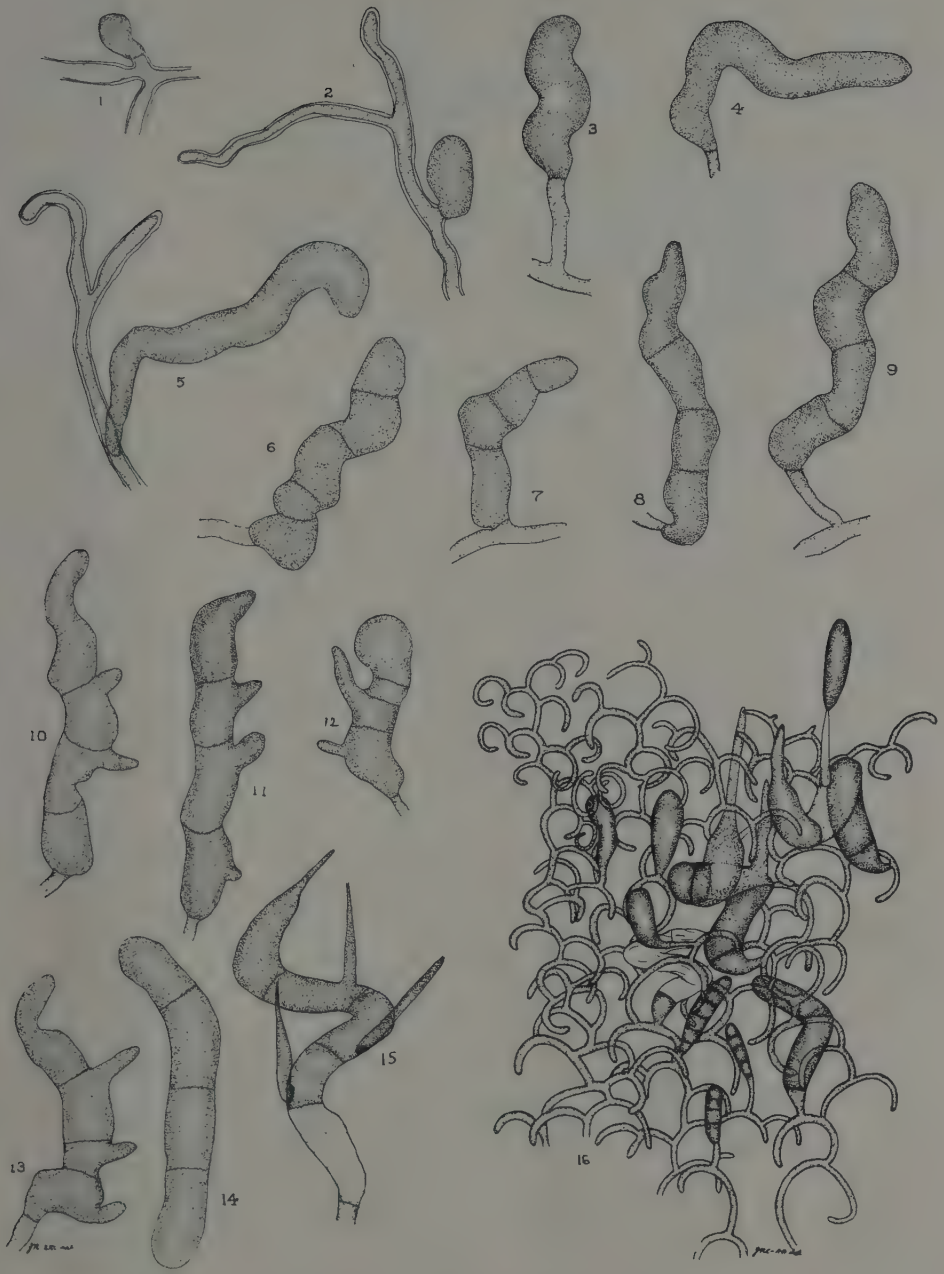
Photograph by Paul F. Shope

PLATE 16



SEPTOBASIDIUM JAMAICAENSE [above]
SEPTOBASIDIUM AREOLATUM [below]

PLATE 17



Septobasidium papyraceum [Figs. 1–14]

Septobasidium frustulosum [Figs. 15, 16]

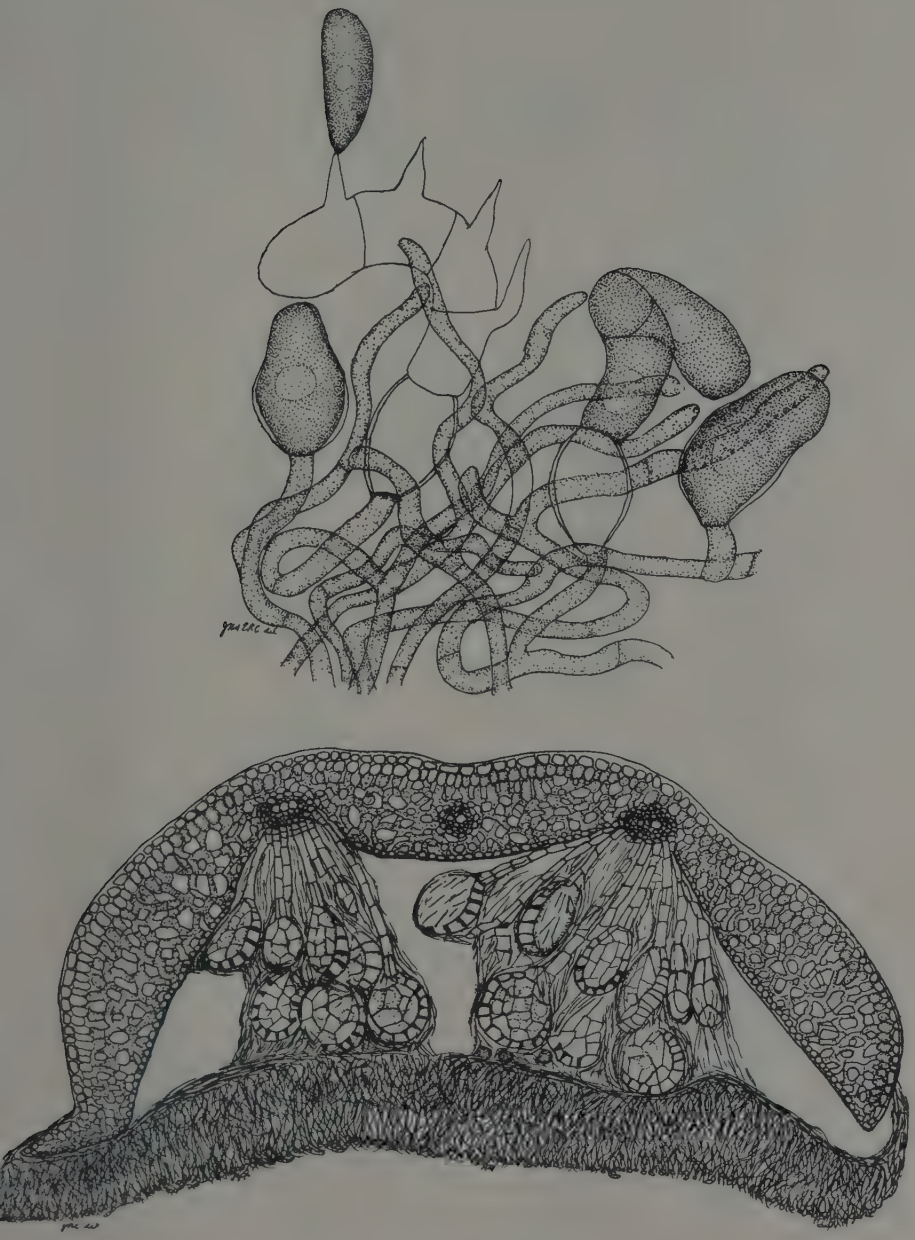
PLATE 18

SEPTOBASIDIUM ATROPUNCTUM

PLATE 19

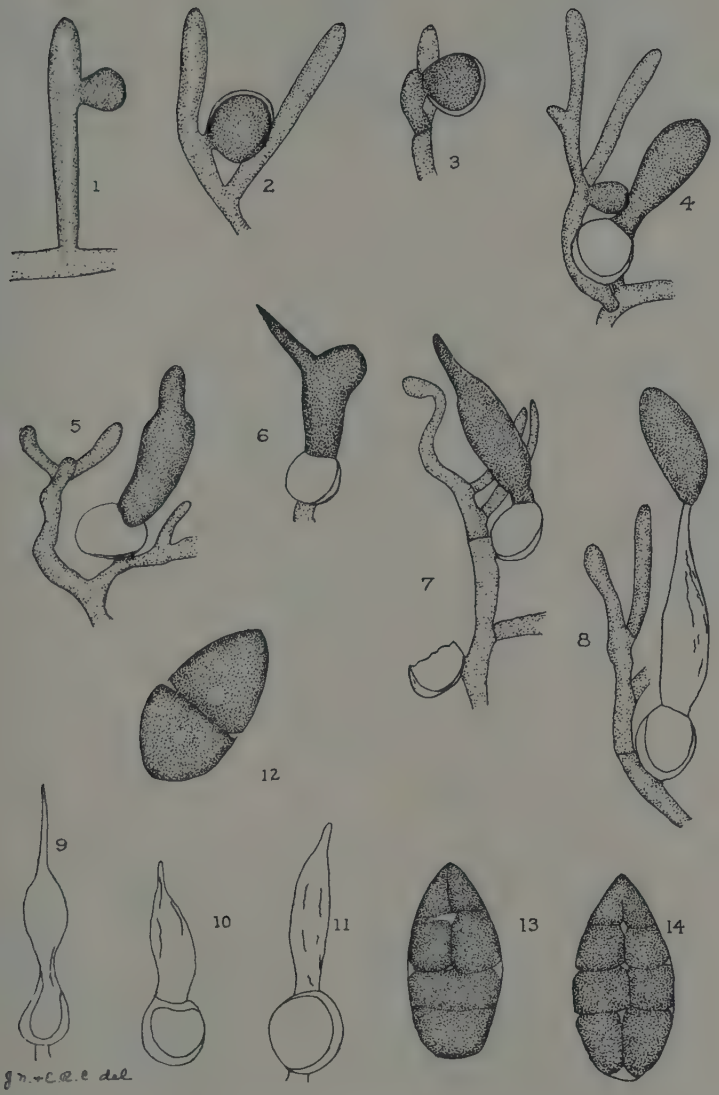
SEPTOBASIDIUM ALVEOLATUM

PLATE 20



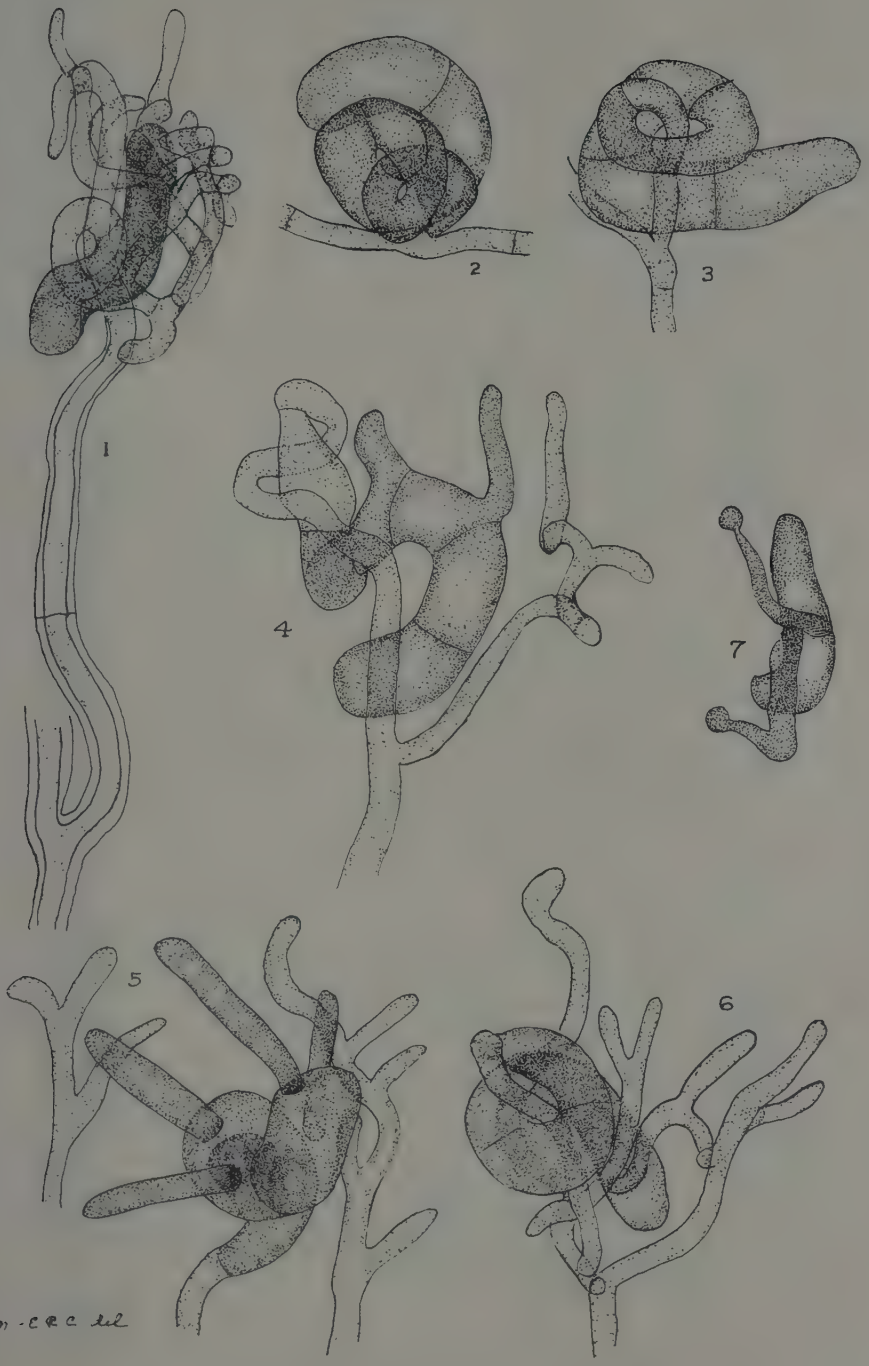
SEPTOBASIDIUM POLYPODII

PLATE 21



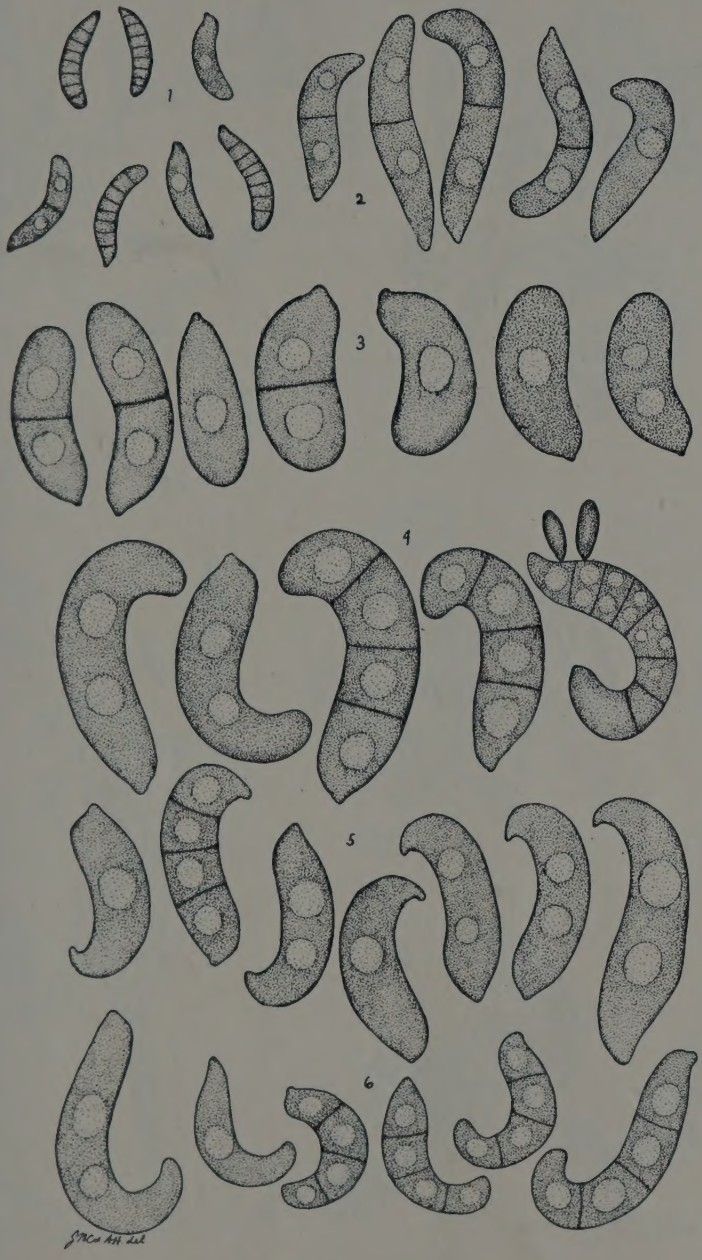
SEPTOBASIDIUM PURPUREUM

PLATE 22



HELICOBASIDIUM ARBOREUM

PLATE 23



SPORES OF VARIOUS SPECIES OF SEPTOBASIDIUM

PLATE 24

TYPES OF HAUSTORIA FROM BODIES OF SCALE INSECTS